ENERGY REQUIREMENTS OF FREE RANGING LITTLE PENGUIN, EUDYPTULA MINOR

DANIEL P. COSTA,* PETER DANN† and WILLIAM DISHER*

*Long Marine Laboratory, Institute of Marine Sciences, University of California, Santa Cruz, CA 95064
†Penguin Reserve Committee of Management, P.O. Box 413, Cowes, Phillip Island, Victoria, Australia 3922

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Abstract—1. Onshore and at sea metabolism and water turnover of Little Blue Penguins, Eudyptula minor, attempting to breed during September 1984 on Phillip Island, Australia, were measured using the doubly-labeled water method.

2. Water influx of two penguins fasting onshore was 18.1 ml/kg·d, with a CO₂ production of 0.903 ml/kg·hr and was estimated to be 1.31 kJ/kg·d or 1.3 times the standard metabolic rate (SMR).

3. Food intake of two penguins at sea was 167 g/kg·d or 855 kJ/kg·d of anchovies and pilchards estimated from a mean water influx of 146 ml/kg·d.

4. CO₂ production of these two birds while onshore and at sea was 1.479 ml/kg·hr or 916 kJ/kg·d, 2.2 times the estimated SMR.

5. The at-sea metabolism estimated from activity budgets and metabolic data of birds onshore and of birds onshore and at sea was 1124 kJ/kg·d, 2.6 times SMR.

INTRODUCTION

Information on the energetics of free-ranging penguins, the bird group most highly adapted to a marine existence, is limited to measurements on only four species. These are of medium-size, ranging from the 3.2 kg Jackass Penguin (Nagy et al., 1984) and 3.6 kg Macaroni Penguin (Davis et al., 1983), to the 6.2 kg Gentoo Penguin (Davis et al., 1983) and the 13.0 kg King Penguin (Kooyman et al., 1982), which is the second largest species of penguin. In light of the recent interest in the scaling of physiological parameters (Schmidt-Nielsen, 1984; Peters, 1983; Calder 1984), data on the smaller species are of value since the only information on the Little Penguin, *Eudyptula minor*, comes from laboratory studies (Pinsob et al., 1977; Stahel and Nicol, 1982; Baudinette and Gill, 1985). The Little Penguin is the smallest species, weighing on average 1.1 kg. In addition to the intrinsic value of data on the energetics of penguin species covering a significant range of body size, where penguins occur, they are one of the most important avian consumer of marine resources (e.g. Croxall, 1984; Duffy et al., in press). Data on their rates of prey and energy utilization are, therefore, important to assess accurately their role as consumers in pelagic marine communities. Here we report the results of a pilot investigation into the foraging energetics of the Little Penguin using the doubly-labeled water technique.

MATERIALS AND METHODS

Little Penguins, *Eudyptula minor*, were studied at Sumnerland Peninsula, Phillip Island, Victoria, Australia (38°31'S 145°08'E) during September 1984. At-sea metabolism (CO₂ production) and water turnover were measured using the doubly-labeled water method (Lifson and McClintock, 1966; Nagy, 1980; Nagy and Costa, 1980). Measurements were carried out on six pre-breeding adults of both sexes that had been observed in their burrows with a mate on the previous night. Utilizing the low-level enrichment methodology (Schoeler and van Santen, 1982), birds were injected with 4 ml of 15% oxygen-18 water followed by 0.1 M CI tritiated water in 1 ml of sterile saline. After injection, birds were held for 2 hr in small boxes, and were then anesthetized by placing the head in a large plastic jar containing cotton saturated with diethyl-ether. Upon a suitable level of anesthesia, birds were laid on their backs and a 4 ml blood sample was taken via cardiac puncture with a 20 gauge 1½" spinal needle. Body weights were measured to within ± 1 g by placing the anesthetized bird on an electronic top-loading balance. One hour after recovery from anesthesia (recovery occurred within 20–30 min), the birds were returned to their burrows. Burrows were checked daily to determine if the injected birds remained on shore or if they had gone to sea. All captures were completed during night-time inspection of study burrows, carried out several hours after dusk (usually 21:00–22:00). Upon recapture (24–48 hr), birds were returned to the onsite laboratory, anesthetized, weighed and blood sampled and again returned to their burrows. Initial total body water (TBW) was determined by the dilution of tritiated water (HTO) (Nagy and Costa, 1980). Total body water for subsequent samples was estimated by the initial fractional water content multiplied by the body weight at that sampling time. Tritium specific activity was determined by scintillation spectrometry of triplicate aliquots of 200 µl of pure water, vacuum-distilled from serum samples, in 10 ml of Betaphase cocktail (Westchem, San Diego, CA). The specific activity of oxygen-18 water was determined by mass ratio spectrometry (Global Geochemistry, Canoga Park, CA) of pure water distilled from plasma samples. Five additional blood samples were collected from non-experimental birds to determine natural oxygen-18 background variation. Carbon dioxide production and water influx was calculated using the equations presented in Nagy (1980) and Nagy and Costa (1980), assuming an exponentially changing body water pool. To calculate metabolism, a constant of 25.8 J/ml CO₂ was used to convert CO₂ production to energy consumption in feeding birds (calcu-

Estimates of the food intake of foraging birds were derived from water influx data. This assumes that birds do not consume sea water and that the only source of water is from that contained in the prey and produced metabolically. Metabolic water production was calculated from metabolism using 0.026 ml H$_2$O/kg (Schmidt-Nielsen, 1982). Pre-

formed water influx was determined by subtracting meta-

bolic water production from the total water influx as determined from HTO turnover. Net food intake is then total water influx minus metabolic water production divided by the prey water content. The diet of these birds is variable, but the mean composition by weight is 3-10% cephalopods and 90-97% fish; the latter is predominantly anchovy, *Engraulis australis* and pilchard, *Sardinops neopilchardus*, in approximately equal amounts (data from Montague, 1982 reanalysed by Croxall, in press). Complete compositional data are not available for prey of the Little Penguin. However, the caloric and water content of cape anchovy, *Engraulis capensis*, are almost identical to that of pilchards eaten by Little Penguins averaged over the year (Cullen, unpublished data). Therefore, we assumed that a 50% anchovy and 50% pilchard diet would be compositionally similar to cape anchovy, which is 72.7% water, 19.7% protein, 5.2% lipid. This diet would have a metabolizable energy content of 5.13 kJ/g fresh weight. This assumes that 77.9% of the ingested energy is metabolizable by adult penguins (Cooper, 1977; Nagy et al., 1984).

### RESULTS

The mean TBW of the six study birds was 63.2% ± 2.0 SD of their body mass, which was 1091 ± 92 SD. Mean variation in natural $^{18}$O abundance of non-experimental birds was 0.199717 ± 0.000261 SD (N = 5). The initial oxygen-18 enrichment was 0.084679 atom % excess and the lowest level attained was 0.035608 atoms % excess in bird 22047 after 4.7 days. Three of the six study birds (22047, 22092 and 21770) were recaptured. Bird 22047 was recaptured three times. It returned on the fifth day. Bird 22092 went to sea and returned on the second day. Thus we collected data on two birds fasting and two birds foraging (Table 1). Normally, Little Penguins are laying eggs or incubating by September and exhibit a predictable metabolism using 0.026 ml H$_2$O/kJ (Schmidt-Nielsen, 1982). Pre-

formed water influx was determined by subtracting meta-

bolic water production from the total water influx as determined from HTO turnover. Net food intake is then total water influx minus metabolic water production divided by the prey water content. The diet of these birds is variable, but the mean composition by weight is 3-10% cephalopods and 90-97% fish; the latter is predominantly anchovy, *Engraulis australis* and pilchard, *Sardinops neopilchardus*, in approximately equal amounts (data from Montague, 1982 reanalysed by Croxall, in press). Complete compositional data are not available for prey of the Little Penguin. However, the caloric and water content of cape anchovy, *Engraulis capensis*, are almost identical to that of pilchards eaten by Little Penguins averaged over the year (Cullen, unpublished data). Therefore, we assumed that a 50% anchovy and 50% pilchard diet would be compositionally similar to cape anchovy, which is 72.7% water, 19.7% protein, 5.2% lipid. This diet would have a metabolizable energy content of 5.13 kJ/g fresh weight. This assumes that 77.9% of the ingested energy is metabolizable by adult penguins (Cooper, 1977; Nagy et al., 1984).

Despite the small sample size, data for both onshore and at-sea metabolism are remarkably consistent between individuals. The measured energy expenditure (916 kJ/kg-d) is 6% greater than the metabolic energy consumed (855 kJ/kg-d). This is consistent with the observed mass loss of foraging birds. Furthermore, the close correspondence between estimated metabolizable food energy intake and energy expenditure suggests that negligible sea-water drinking occurred. Significant sea-water ingestion would result in overestimates of food intake. Similar estimates of prey and energy consumption suggest negligible sea-water ingestion in Jackass penguins (Nagy et al., 1984) and Grey Headed Albatrosses, *Diomedea chrysostoma* (Costa and Prince, 1986). Laboratory studies on feeding pinnipeds have also demonstrated an absence of sea-water drinking (Depocas et al., 1970; Costa and Gentry, 1986; Costa, 1984).

Croxall (1982) estimated the metabolic cost of incubation in six species of medium to large penguins using weight loss data from fasting and incubating birds. We can compare the metabolic rate measured in fasting Little Penguins with the values predicted from Croxall's (1982) regression equations. Assuming that all of the mass lost was fat, a mean 1106 g Little Penguin would consume 678 kJ/kg-d; if only 55.5% of the mass loss was fat, they would utilize 544 kJ/kg-d. The measured mean value of 560 kJ/kg-d is within 3% of this latter value (544 kJ/kg-d), supporting Croxall's (1982) prediction of a mixed metabolism.

The field metabolic rate (FMR) of Little Penguins measured in this study (2.2 × SMR) is lower than Jackass *Spheniscus demersus* (2.6 × SMR) (Nagy et al., 1984), *King Aptenodytes patagonica* (? 6 × SMR) (Kooyman et al., 1982), Gentoo *Pygoscelis papua* (2.6 × SMR) and Macaroni *Eudyptes chrysolophus*.

### Table 1

<table>
<thead>
<tr>
<th>Animal no.</th>
<th>Initial (g)</th>
<th>Final (g)</th>
<th>Time (days)</th>
<th>Mass (g/d)</th>
<th>Water influx (ml/kg-d)</th>
<th>Metabolism (ml CO$_2$ g/hr)</th>
<th>(kJ/kg-d)</th>
<th>FMR/SMR</th>
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</thead>
<tbody>
<tr>
<td>Fasting</td>
<td></td>
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<td></td>
<td></td>
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<td></td>
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<tr>
<td>No. 22092</td>
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<td>1023</td>
<td>3.203</td>
<td>34</td>
<td>18.0</td>
<td>0.968</td>
<td>599</td>
<td>1.41</td>
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<tr>
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<td>1094</td>
<td>2.720</td>
<td>30</td>
<td>18.5</td>
<td>0.839</td>
<td>520</td>
<td>1.22</td>
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<tr>
<td>Mean</td>
<td>1154</td>
<td>1058</td>
<td>2.961</td>
<td>32</td>
<td>18.1</td>
<td>0.903</td>
<td>560</td>
<td>1.31</td>
</tr>
<tr>
<td>At sea</td>
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<td></td>
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<td></td>
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<tr>
<td>No. 22047</td>
<td>1094</td>
<td>1053</td>
<td>2.026</td>
<td>20</td>
<td>144.0</td>
<td>1.435</td>
<td>899</td>
<td>2.00</td>
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<tr>
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<td>1.894</td>
<td>34</td>
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<td>1.523</td>
<td>943</td>
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<tr>
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<td>1050</td>
<td>1.960</td>
<td>27</td>
<td>145.5</td>
<td>1.479</td>
<td>916</td>
<td>2.15</td>
</tr>
</tbody>
</table>

The metabolic rate was calculated from CO$_2$ production. Field metabolic rate (FMR) divided by the SMR measured for this species (Stahl and Nicol, 1982) is given for comparison.
(2.9 \times \text{SMR}) \ (\text{Davis et al., 1983}) \ \text{Penguins. However, these studies included both onshore and at-sea components in the FMR measurement. A more interesting comparison may be gained by examining only the cost incurred while at sea. An estimate of the FMR at sea can be derived from observations of Little Penguin onshore–offshore movements. During this study 99\% of all penguins at the colony arrived in the first hour after dusk (18:30 hr). Ninety-nine percent of all departures occurred during the hour before dawn (05:00 hr). Therefore, most birds spent 9.5 hr ashore (09:00 to 04:30 hr) \ (\text{Reilly, 1984}).

From Table 1, the cost of fasting in burrows is 550 \text{kJ/kg} \text{d} and, therefore, in a 24-hr period, the energy expended onshore is 22 \text{kJ/kg} \ (9.5 \text{hr onshore} \times 23.3 \text{kJ/kg} \text{hr}). Subtracting this cost from the overall FMR yields the metabolic expenditure during 14.5 hr at sea (901 \text{kJ/kg} \times 221 \text{kJ/d}). Thus, the daily at-sea metabolic rate is 1124 \text{kJ/kg} \text{d} or 2.6 times SMR. Similar field measurements are only available on Jackass Penguins, which expend 6.6 times SMR while at sea \ (\text{Nagy et al., 1984}). However, laboratory data on penguin swimming energetics are surprisingly similar to our field measurements. Little Penguins swimming in a water flume expend 2.5 times SMR \ (\text{Baudinette and Gill, 1985}) while Peruvian Penguins expend 3.1 times SMR \ (\text{Hui, 1983}).

\text{Nagy et al., 1984} defined an estimate of the foraging efficiency (FE) of Jackass Penguins as the metabolic energy expended at sea to acquire the total assimilated energy necessary for the trip at sea and time onshore. Such a calculation includes only the energy consumed by the adult for its own maintenance. A similar measure of FE can be derived for Little Penguins using the same data described above. We know that 680 \text{kJ/d} are expended to collect 855 \text{kJ}. Therefore, the FE is 1.36 \ ((855/680)) \text{kJ/kg} \text{d}, considerably lower than the 2.1 calculated for Jackass Penguins \ (\text{Nagy et al., 1984}). Variability in FE may indicate changes in prey abundance or availability \ (\text{Nagy et al., 1984}). Our FE estimate for Little Penguins is low when compared to Jackass Penguins; however, the Little Penguins lost weight even while foraging. The weights of our experimental birds \ (\text{mean = 1096 g}) and those of others in the Summerland Peninsula colony \ (\text{mean 1039 g}) were 6–18\% lower than for the same period in the previous two years \ (\text{Sept 1982, mean 1256 g; Sept 1983, mean 1184 g}). Further, the 1984 breeding season saw an increase in adult mortality, a late start, a short duration and a very low fledging success \ (\text{Dann, in prep}). The low FE we report for Little Penguins may indicate the paucity of prey items during the 1984 season and, perhaps, the reason for the devastating reduction in breeding success that year.

Additional research is needed to adequately assess the free-ranging energetics of Little Penguins. However, the data presented here do give a preliminary indication of field metabolic rates of the smallest penguin. Despite its small size, the energy requirements of the Little Penguin do not appear to be markedly different from those reported for larger penguin species. Future studies incorporating the double-labeled water methodology with data on diet, proximate composition of prey, individual attendance patterns of birds, swim velocity and direction would allow a complete analysis of the foraging energetics of this species.

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